

# The larval development of the spider crab *Rochinia carpenteri* (Thomson) [Oxyrhyncha : Majidae] with a review of majid subfamilial larval features

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## Synopsis

Two zoeal and a megalopal stage of the N.E. Atlantic deepwater spider crab *Rochinia carpenteri* are described from laboratory-reared material. Subfamilial larval features of the Majidae are reviewed and the larval affinities of *R. carpenteri* are discussed.

## Introduction

The deepwater spider crab *Rochinia carpenteri* (Thomson) has been recorded from S. Iceland to N.W. Africa (Christiansen, 1969 : 123) and in depths from about 180 to 1258 m (Hansen, 1908 : 12) on sandy chalk mud (Thomson, 1874 : 176).

In October 1977, five ovigerous crabs were trawled from the Rockall Trough/Hebridean Terrace region of the N.E. Atlantic ocean and transported to the British Museum (Natural History). The larvae hatched by two of these females were successfully reared to the megalopal stage and provide material for the first description of the larval stages of this genus and species.

## Materials and methods

The ovigerous crabs were trawled in the Rockall Trough/Hebridean Terrace region of the N.E. Atlantic ocean in the following positions: (a) 56°23·1' N: 09°18·2' W, 1010–1030 m, Agassiz trawl towed 30 min on 20.10.1977; (b) 56°31·7' N: 09°13·2' W–56°29·4' N: 09°11·3' W, 780–710 m, single warp trawl towed 2 h 28 min on 22.10.1977.

Larvae were reared using methods described by Rice & Ingle (1975 : 104) and Ingle & Clark (1977). Material was fixed in Steedman's solution (Steedman, 1976 : 148) and later transferred to 70% IMS. Drawings and measurements were made with the aid of a *camera lucida*. Measurements given under *Descriptions* are: (a) distance between tips of dorsal and rostral spines (T.T.); (b) carapace length, from between the eyes to the postero-lateral carapace margin (C.L.). The material has been registered as BM(NH) 1978: 282–3.

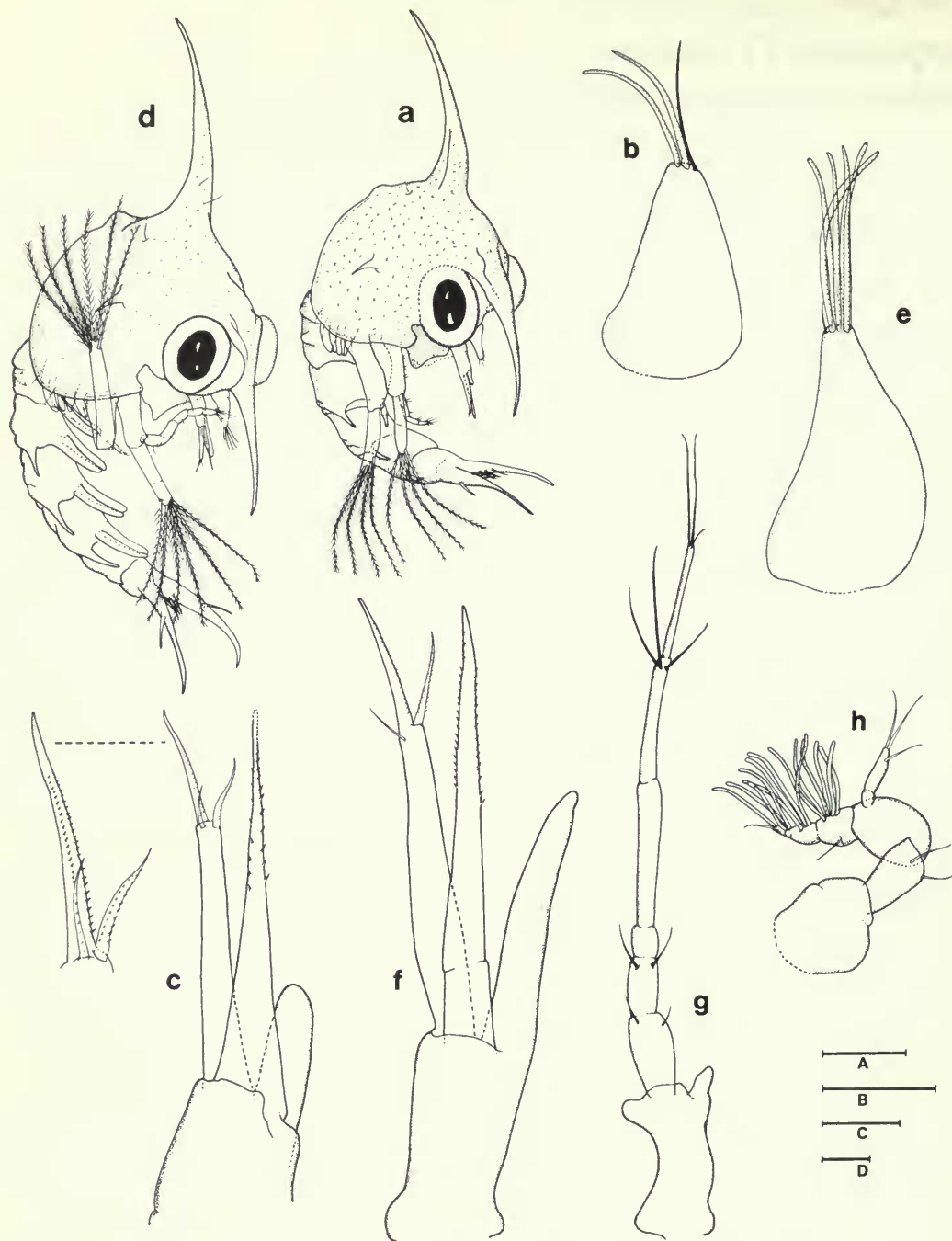
## Results

Hatching occurred between 16 and 20 January 1978. An average of 36 days elapsed between hatching and the appearance of megalops. Only a small number of second-stage zoeae successfully moulted to the megalopal stage.

## Descriptions

### First zoea

DIMENSIONS: T.T. 2·3–3·5 mm; C.L. 1·0–1·2 mm.



**Fig. 1** *Rochinia carpenteri*: (a)–(c) zoea I; (d)–(f) zoea II; (a), (d) lateral aspect, scale A = 0.5 mm; (b), (e) antennule, scale B = 0.1 mm; (c), (f) antenna, scale C = 0.1 mm; (g), (h) megalopa, antennule & antenna respectively, scale D = 0.1 mm.

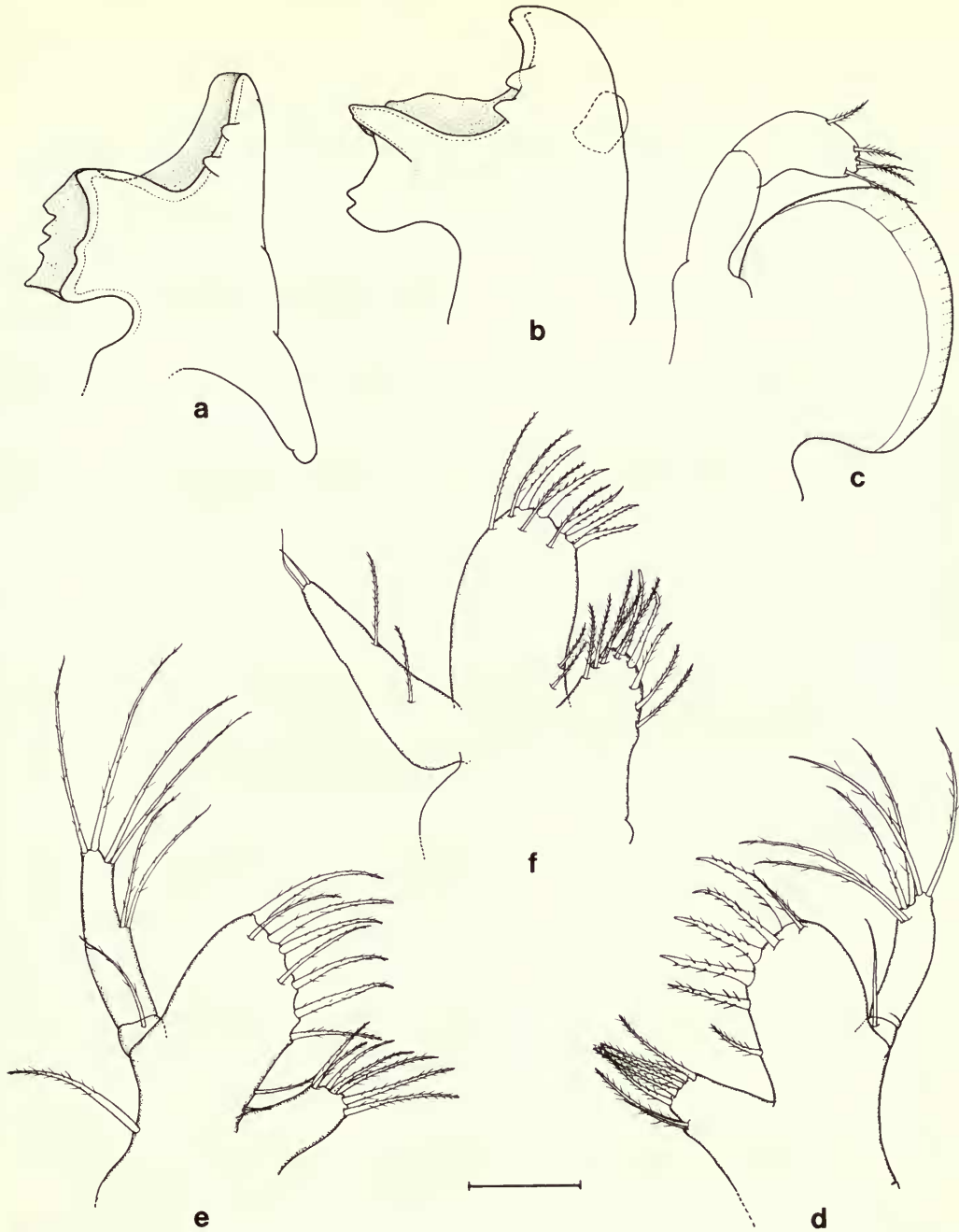


Fig. 2 *Rochinia carpenteri*: ventral aspects of: mandible (a) zoea I, (b) zoea II, (c) megalopa; maxillule (d) zoea I, (e) zoea II, (f) megalopa; scale = 0.1 mm.

**CARAPACE** (Fig. 1a): Surface punctate, dorsal and rostral spines well developed, slightly curved, narrowing distally; lateral spines well developed. A prominent, broad, median postero-dorsal tubercle and a pair of posteriorly placed setae; dorso-median elevation of carapace well developed; postero-lateral margin with a few long spinules arising from inner surface.

**EYES**: Partly fused to carapace.

ANTENNULE (Fig. 1b): Unsegmented, with 2 terminal aesthetascs and one long seta.

ANTENNA (Fig. 1c): Distal half of spinous process spinulate; exopod reaching well into distal half of spinous process, with 3 terminal spines, longest reaching to apex (or slightly beyond) of spinous process; endopod slightly more than half length of exopod.

MANDIBLE (Fig. 2a): Incisor and molar processes well developed, palp absent.

MAXILLULE (Fig. 2d): Endopod 2-segmented, with 1, 6 setae respectively; distal margin of basal endite with 5 setose spines and 1 seta, inner margin with 1 seta; coxal endite with 7 setae.

MAXILLA (Figs 3a, b): Endopod with large outer and small indistinct inner lobe with 3 + 3 setae; basal endite with large outer and smaller inner lobe with 4 + 5 setae; coxal endite bilobed with 4 + 5 setae; scaphognathite with 12 marginal setae.

FIRST MAXILLIPED (Fig. 4a): Basis with 10 setae (arranged 2, 2, 3, 3); endopod 5-segmented with 3, 2, 1, 2, 4 + 1 setae; exopod incipiently 2-segmented (in some specimens) with 4 terminal natatory setae.

SECOND MAXILLIPED (Fig. 4c): Basis with 3 setae; endopod 3-segmented, 1st and 2nd segments indistinct, in some specimens, with 0, 1, 4 + 1 setae; exopod incipiently 2-segmented, with 4 terminal natatory setae.

THIRD MAXILLIPED AND PEREIOPODS: Represented as incipient buds.

ABDOMEN (Figs 5a, b): 5-segmented + telson; second segment with a pair of outwardly directed broad-based, curved, dorso-lateral processes; postero-lateral processes on segments 3–5 acute, decreasing slightly in size on successive segments, those on fifth angled downwards. A pair of minute setae near postero-dorsal margin of each segment. Telson forks long, curved and spinulate, each with one long lateral spine; inner posterior margin of telson straight or slightly convex, with 3 pairs of long, plumed setae.

### Second zoea

DIMENSIONS: T.T. 3.0–3.2 mm; C.L. 1.3–1.5 mm.

CARAPACE (Fig. 1d): Dorsal spine with few setae near base; postero-dorsal tubercle larger than in first stage.

EYES: Stalked.

ANTENNULE (Fig. 1e): With 5 aesthetascs and one short seta.

ANTENNA (Fig. 1f): Longest of 3 spines on exopod reaching well beyond distal extremity of spinous process; endopod much more than half length of exopod.

MANDIBLE (Fig. 2b): Molar process longer than in first stage; unsegmented mandibular palp developed.

MAXILLULE (Fig. 2e): Outer margin of basal endite with prominent plumose seta, distal margin with 6 spines and 2 setae, inner margin with 2 setae; coxal endite with 6–7 setae.

MAXILLA (Fig. 3c): Endopod with 4 + 3 setae; basal endite with 8 + 5 setae; scaphognathite with 21–23 setae.

FIRST MAXILLIPED (Fig. 4b): Exopod with 6 terminal natatory setae.

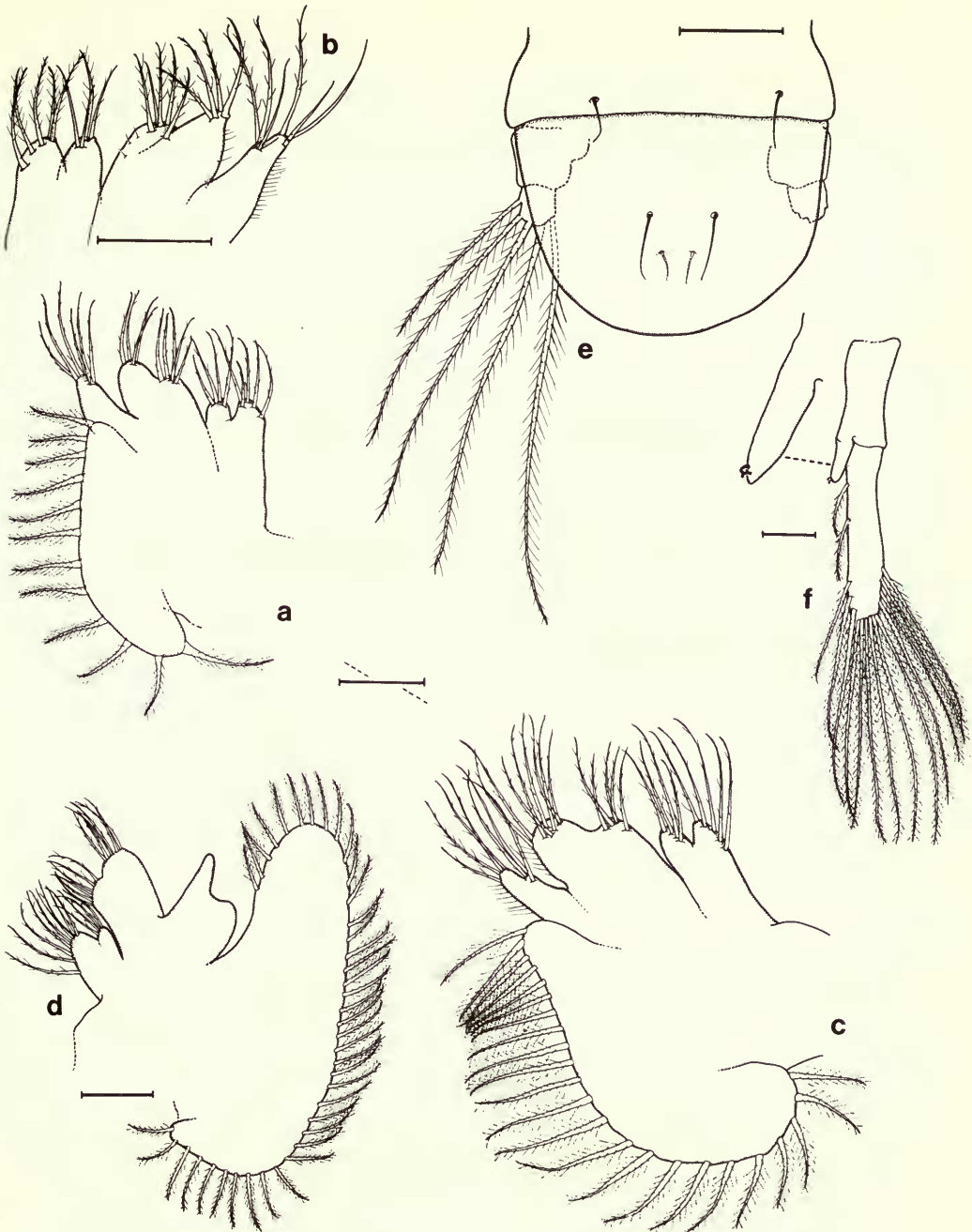
SECOND MAXILLIPED (Fig. 4d): Exopod with 6 terminal natatory setae.

THIRD MAXILLIPED AND PEREIOPODS: Represented as incompletely segmented buds.

ABDOMEN (Figs 5c, d): 6-segmented, 6th segment with acute postero-ventral margin. Additional pairs of minute dorsal setae on segments 3–4 and sometimes on 5; pleopod buds well developed on segments 2–5.

### Megalopa

DIMENSIONS: C.L. 2.3–2.5 mm.



**Fig. 3** *Rochinia carpenteri*: maxilla (a) zoea I, (b) terminal portion from another specimen, (c) zoea II, (d) megalopa; (e) telson and left uropod and (f) 1st pleopod of megalopa; scales = 0.1 mm.



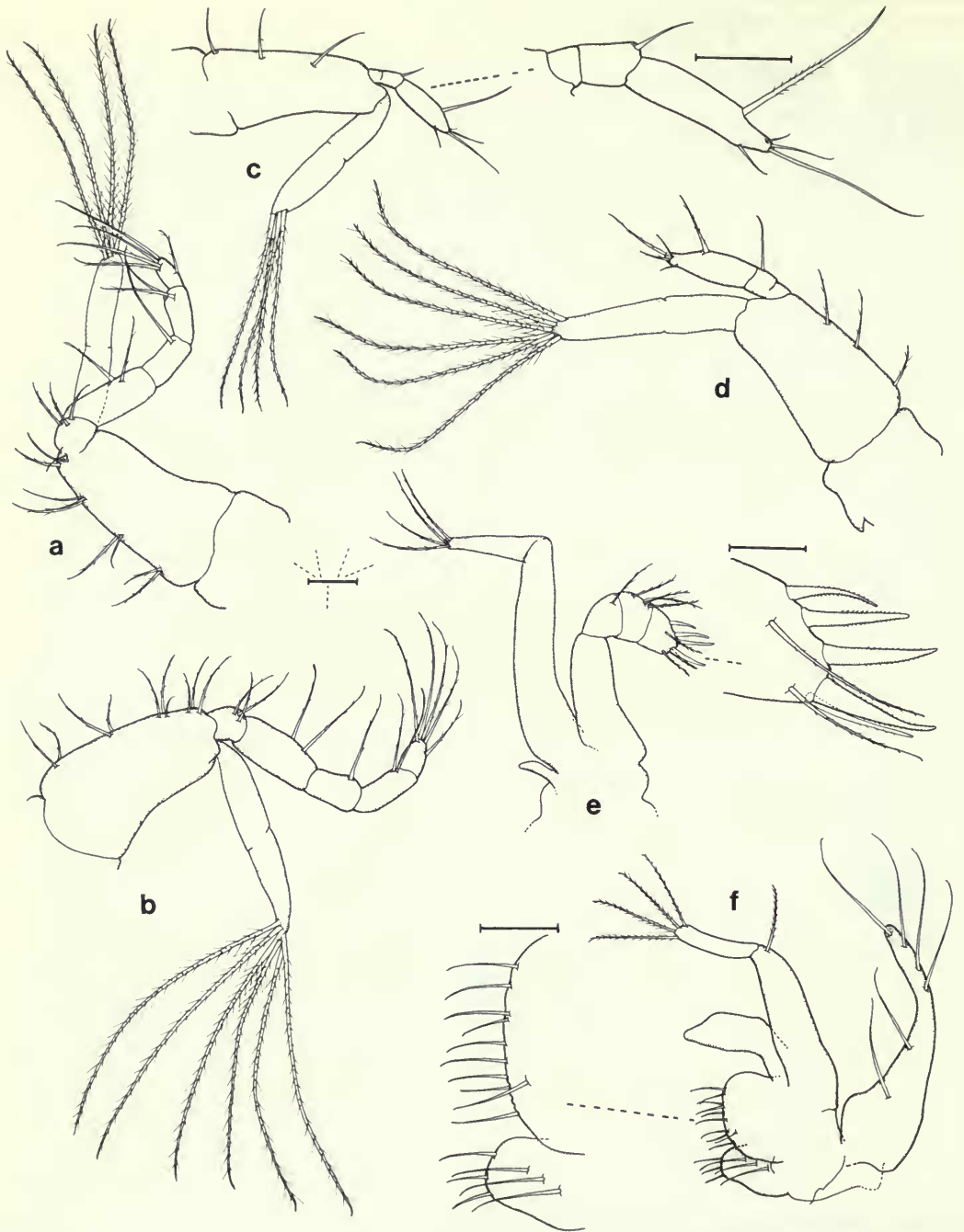


Fig. 4 *Rochinia carpenteri*: 1st maxillipeds (a) zoea I, (b) zoea II, (f) megalopa; 2nd maxillipeds (c) zoea I, (d) zoea II, (e) megalopa; scales = 0.1 mm.

**CARAPACE** (Figs 7c, d): Longer than broad, anteriorly setose, rostrum long; hepatic regions inflated, each protogastric region with a cristate tubercle; a longitudinal carina on each epibranchial region ending posteriorly in a cristate process; a pair of carinae on metagastric region; each epibranchial/mesobranchial region with an obliquely placed carinae; a very long, stout, median cardiac spine and a small median marginal intestinal tubercle.

**EYES:** Large, with well-developed cornea.

**ANTENNULE** (Fig. 1h): Peduncle 3-segmented, 2nd segment with two distally placed setae; exopod with 4–5 incomplete segments, second with 6 aesthetascs, 3rd with 4, 4th with 3, 5th with one aesthetasc and one seta; endopod 2-segmented, distal segment with 3 setae.

**ANTENNA** (Fig. 1g): Peduncle 3-segmented, first segment with outer lower distal margin produced as acute process, inner upper distal margin with sub-acute expansion; second and third peduncle segments each with 2 distal dorsal median setae; flagellum 4-segmented, third and fourth segments each with 3 setae.

**MANDIBLE** (Fig. 2c): Incisor process expanded as broad plate with sharp margins, molar process reduced; mandibular palp large, 2-segmented, proximal segment longer than distal, distal with 5 plumose setae.

**MAXILLULE** (Fig. 2f): Endopod reduced, segmentation indistinct, with 4 setae; distal margin of basal endite with 5–6 setosed spines and 4 setae; coxal endite with 10 setae.

**MAXILLA** (Fig. 3d): Endopod reduced, basal endite with 6+6 setae, coxal endite with 3–4+9 setae.

**FIRST MAXILLIPED** (Fig. 4f): Coxa with 6, basis with 10 setae arranged longitudinally. Exopod 2-segmented, proximal with one and distal segment with 4 terminal setae; endopod reduced, unsegmented; epipod well developed, with 6 long setae.

**SECOND MAXILLIPED** (Fig. 4e): Exopod 2-segmented, distal segment about half length of proximal and with 4 terminal setae; endopod 4-segmented, 2nd segment (carpus) with one and third (propodus) with 4 setae, 4th segment (dactylus) with 4 spines and 3 setae; epipod small.

**THIRD MAXILLIPED** (Fig. 6a): Coxa/basis with a transverse row of setae. Endopod 5-segmented, inner margin of ischium with irregular serrations, outer surface with 13–15 short setae; outer margin of merus with 2, ventral with 4–5 setae, carpus and propodus with 5 distally placed setae respectively, dactylus with 4 terminal setae. Exopod 2-segmented, distal segment about half length of proximal and with 6–7 terminal setae. Epipod with 5 long setae.

**PEREIOPODS** (Figs 6b–d, 7a, b): Chelipeds moderately stout, setosed, inner propodal margin with several cristate teeth, inner dactylar margin cristate. Pereiopods 2–5 moderately stout, setosed, dactylus terminally thin and curved, inner margin with 3 spines; pereiopods 2–4 with a coxal and ischial spine.

**ABDOMEN** (Fig. 5e): 6-segmented+telson; with 1–2 pairs of postero-dorsal setae; postero-lateral margins of segments rounded, first often with 1–2 setae. Telson broader than long (Fig. 3e), with a pair of dorsal and ventral median setae. Five pairs of pleopods, exopod of first (Fig. 3f) to fourth with 14–16 marginal plumose setae; endopod with 2 coupling hooks; exopod of fifth pleopod (uropod) with 5 long plumose setae.

### Review of subfamilial larval features of the Majidae

Larval relationships of genera and species in the Majidae have been discussed by Cano (1893), Lebour (1928, 1931), Aikawa (1937), Bourdillon-Casanova (1960), Yang (1968), Kurata (1969), Italo Campodonico & Leonardo Guzman (1972) and Yang (1976); some studies still await publication (Yang, 1967). There would seem little point in attempting further phylogenetic evaluations until descriptions of the larvae of many more majids become available, particularly of species belonging to the subfamily Majinae, of which only five species have been described, and of the Ophthalmiinae, of which the larval stages of only one species is known. Despite this

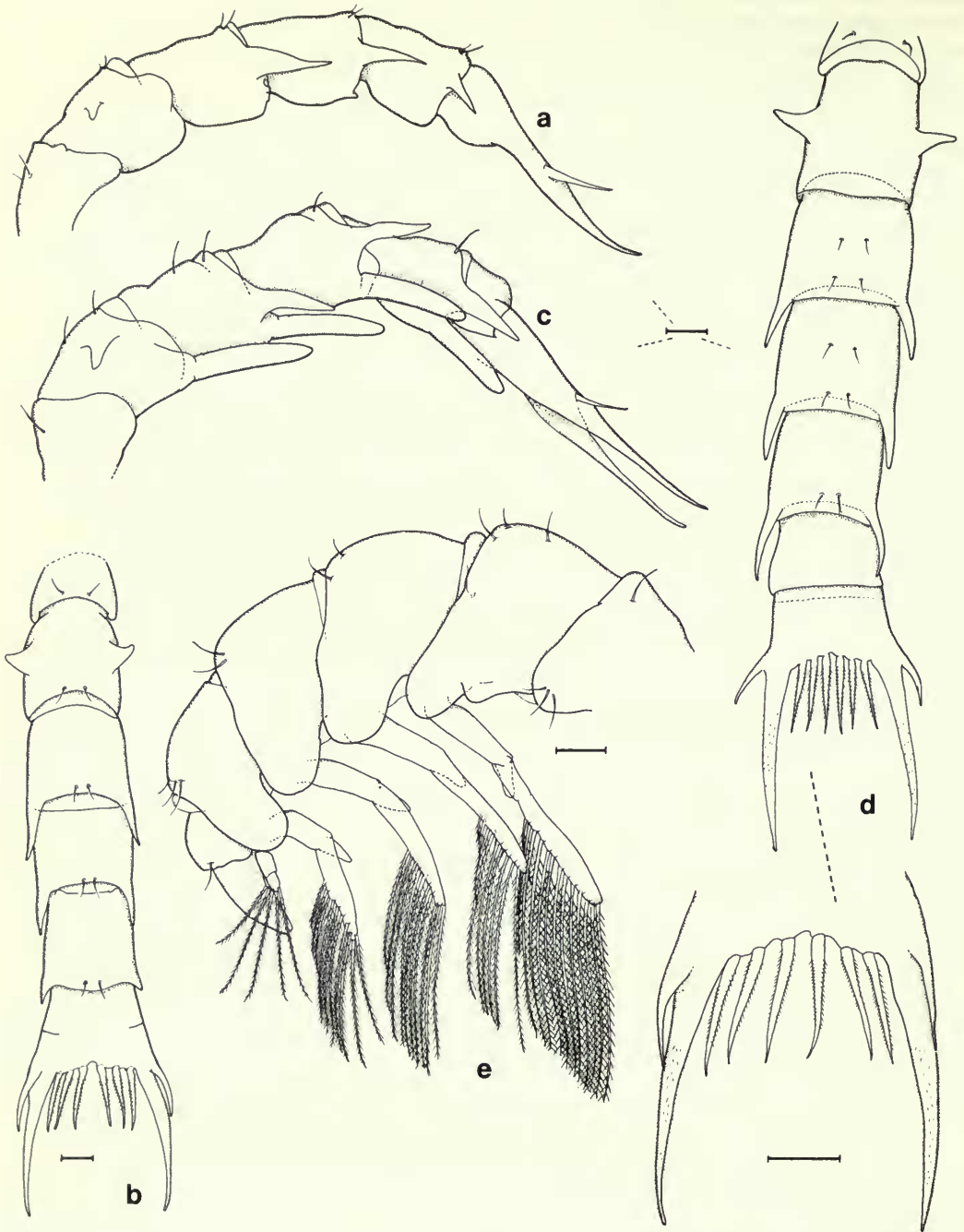


Fig. 5 *Rochinia carpenteri*: abdomens, lateral and dorsal aspects (a), (b) zoea I, (c), (d) zoea II (lower inset of another specimen), (e) megalopa lateral aspect; scales = 0.1 mm.



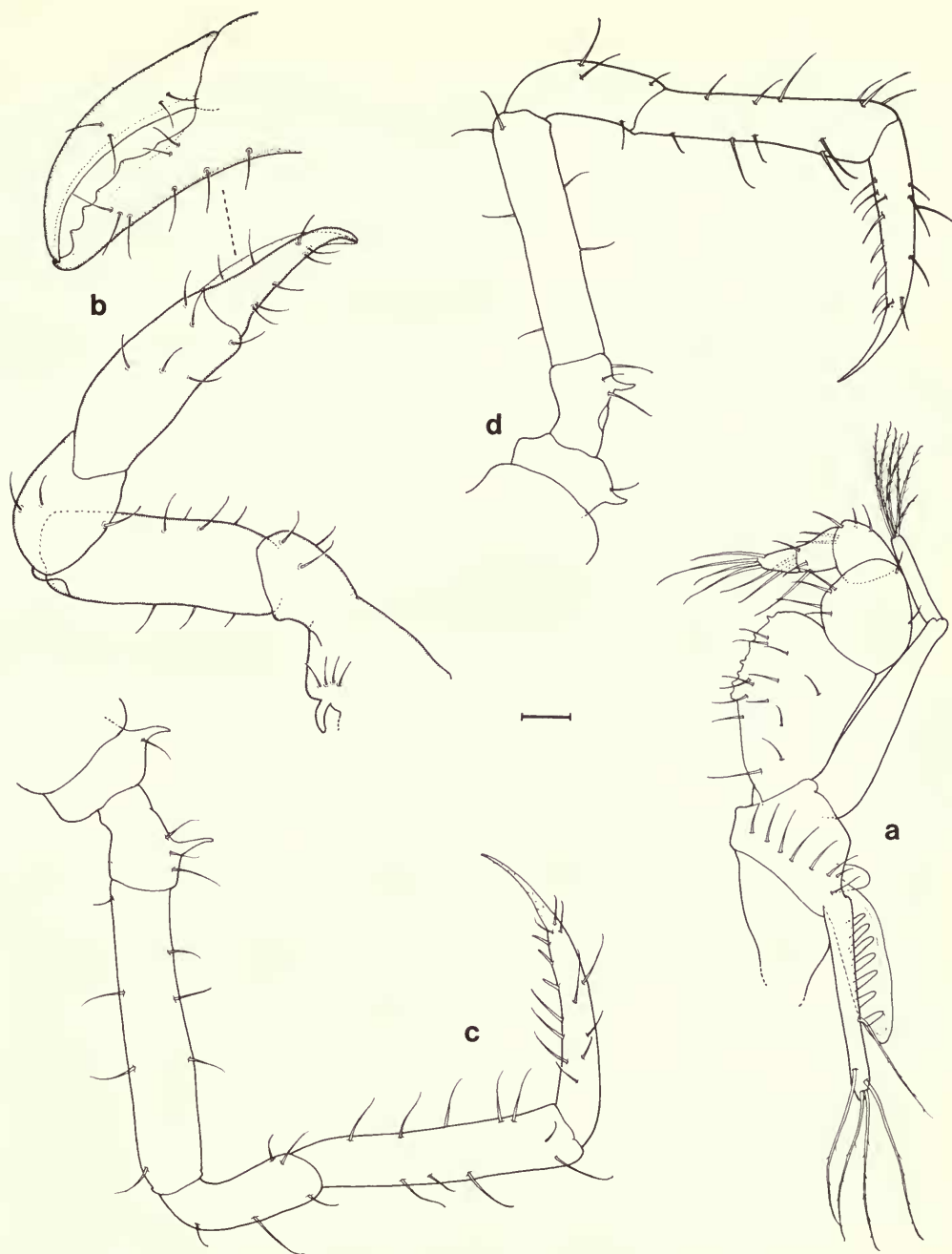


Fig. 6 *Rochinia carpenteri*: megalopa (a) 3rd maxilliped, (b) cheliped, (c) 2nd pereopod, (d) 3rd pereopod; scale = 0.1 mm.

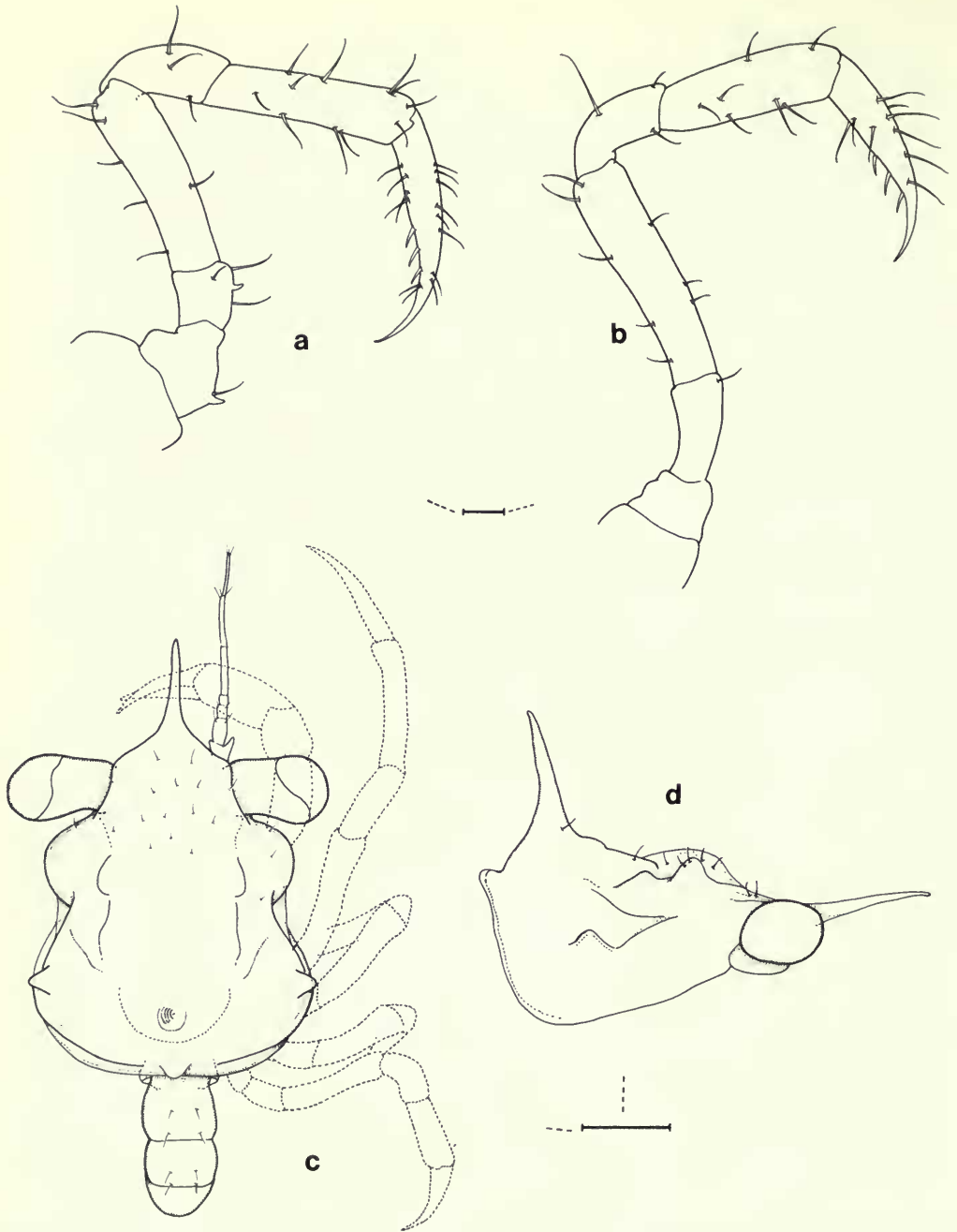


Fig. 7 *Rochinia carpenteri*: megalopa (a) 4th pereiopod, (b) 5th pereiopod, (c) dorsal and (d) lateral aspects of carapace; scales, upper = 0.1 mm, lower = 0.5 mm.

incompleteness it would seem useful to attempt an evaluation of larval characteristics described to date for the Majidae to discover the degree of larval homologies that exist within the currently accepted subfamilial (see Griffin, 1966) classification of the adults. In this appraisal only features are considered that have been sufficiently well illustrated or described for the majority of majid zoeae and megalopae. Some of these (i.e. setation on basal segment of the maxillipeds of zoeae and the presence or absence of pereopod coxal spines of the megalopae) as well as other features that are not listed here (i.e. setal armature of the maxillule and of the first and second maxilliped endopod of the zoeae) may eventually prove to be of considerable importance, when used in combination with other features, for separating the subfamilies. In general, these above-mentioned features are poorly documented for the majority of previously described majid larvae and only a limited amount of material has been available for verifying some of these features during the course of this present study. A larval bibliography of the Majidae, resulting from this literature appraisal, is given on pp. 59-63.

#### Subfamily OREGONIINAE

**ZOEA:** Carapace lateral spines present; dorsal and rostral spines very long; more than one spine<sup>1</sup> on each telson fork; dorso-lateral processes on 2nd and 3rd abdominal segments; posterior-lateral abdominal processes on 3rd-5th segments often very long; basal segment of 2nd maxilliped with 4-5 setae; antennal exopod with terminal setae.<sup>2</sup>

**MEGALOPA:** Rostrum present, not strongly deflected ventrally; submedian spines (carapace spines behind eyes) present; a single or a pair of prominent cardiac spines; basal segment of 2nd pereopod with a spine; uropods present.

**GENERA:** *Chionoecetes*, *Hyas*, *Oregonia*.

#### Subfamily ACANTHONYCHINAE

**ZOEA:** Carapace lateral spines absent; dorsal and rostral spines very short or absent; only one spine<sup>1</sup> on each telson fork; dorso-lateral processes on 2nd, rarely on 3rd (? *Menaethius*) abdominal segment; posterior-lateral abdominal processes on 3rd-5th segments short or absent; basal segment of 2nd maxilliped with 2-3 marginal setae; antennal exopod with sub-terminal<sup>3</sup> setae.

**MEGALOPA:** Rostrum present, strongly deflected ventrally or reduced in size; submedian spines absent; cardiac spine sometimes absent or reduced; basal segment of 2nd pereopod? without a spine; uropods present.

**GENERA:** *Acanthonyx*, *Epialtus*, *Huenia*, *Menaethius*, *Pugettia*, *Taliepus*.

#### Subfamily INACHINAE

**ZOEA (group I):** Carapace lateral spines absent; dorsal spine of moderate length, sometimes long; rostral spine absent, rarely present (*Naxia*); only one spine<sup>1</sup> on each telson fork; dorso-lateral processes on 2nd, rarely on 3rd (*Stenorhynchus*) abdominal segment; posterior-lateral abdominal processes on 3rd-5th segments sometimes long; basal segment of 2nd maxilliped with not more than 3 marginal setae; antennal exopod with sub-terminal<sup>3</sup> setae.

**MEGALOPA (group I):** Rostrum absent (present only in *Stenorhynchus* and strongly deflected ventrally); submedian spines often well developed (except in *Anasimus*); cardiac spines small or absent (except in *Stenorhynchus*); some abdominal segments with dorsal spinules or spinules (except in *Stenorhynchus*); basal segment of 2nd pereopod ? with or without a spine; uropods absent or vestigial (except in *Stenorhynchus*).

**GENERA:** *Achaeus*, *Anasimus*, *Inachus*, *Macropodia*, *Naxia*, *Stenorhynchus*.

<sup>1</sup> Distinction is not made here between lateral and dorsal spines or spinules as this difference is not always clearly shown in some illustrations.

<sup>2</sup> This implies that the exopod terminates in 2 or 3 spines or setae of equal thickness but not necessarily of equal length.

<sup>3</sup> This implies that the exopod terminates in a short movable or non-movable stout spine from the base of which arise one or two setae, usually shorter than the length of the spine.

ZOEA (group II): Carapace lateral spines present; dorsal spine of moderate length; rostral spine of moderate length often short; more than one spine<sup>1</sup> on each telson fork; dorso-lateral processes on 2nd and 3rd abdominal segments; postero-lateral abdominal processes on 3rd–5th segments sometimes short; basal segment of 2nd maxilliped with not more than 3 marginal setae; antennal exopod with terminal<sup>2</sup> setae.

MEGALOPA (group II): Rostrum present, strongly deflected ventrally or straight; submedian spines developed or reduced; cardiac spine short or long; abdominal segments without dorsal spines; basal segment of 2nd pereopod with or ? without spines; uropods present.

GENERA: *Eurypodius*, *Macrocheira*, *Pleistacantha*, *Camposcia*.

#### Subfamily PISINAE

ZOEA: Carapace lateral spines absent; dorsal spine of moderate length; rostral spine of moderate length often short; only one spine<sup>1</sup> on each telson fork; dorso-lateral processes on 2nd abdominal segment, rarely on 3rd (*Herbstia*); postero-lateral processes on 3rd–5th abdominal segments often short; basal segment of 2nd maxilliped with not more than 3 marginal setae; antennal exopod with sub-terminal<sup>3</sup> setae.

MEGALOPA: Rostrum present often straight; submedian spines absent; cardiac spine absent (except in *Libinia*); basal segment of 2nd pereopod without a spine; uropods present.

GENERA: *Eurynome*, *Herbstia*, *Hyastenus*, *Libidoclaea*, *Libinia*, *Lissa*, *Naxioides*, *Pisa*, *Pisoides*.

#### Sub family MAJINAE

ZOEA (group I): Carapace lateral spines present; dorsal spine often well developed and usually of moderate length; rostral spine prominent, of moderate length; more than one spine<sup>1</sup> on each telson fork; dorso-lateral processes on 2nd and 3rd abdominal segments (? absent on 3rd in *Maja verrucosa*); postero-lateral processes on 3rd–5th abdominal segments prominent sometimes long; basal segment of 2nd maxilliped with not more than 3 marginal setae; antennal exopod with terminal<sup>2</sup> setae.

MEGALOPA (group I): Rostrum present and moderately well developed, slightly deflected ventrally; submedian spines or processes present; cardiac spine not prominent; basal segment of 2nd pereopod with spines; uropods present.

GENERA: *Maja*, *Schizophrys*.

ZOEA (group II): Carapace lateral spines absent; dorsal spine sometimes reduced or absent; rostral spine sometimes reduced; more than one spine<sup>1</sup> on each telson fork; dorso-lateral processes only on 2nd abdominal segment; postero-lateral processes on 3rd–5th abdominal segments sometimes short; basal segment of 2nd maxilliped ? with not more than 3 marginal setae; antennal exopod with terminal<sup>2</sup> setae.

MEGALOPA (group II): Rostrum present, sometimes small; submedian spines or processes sometimes absent; cardiac spine small; basal segment of 2nd pereopod with a spine; uropods present.

GENERA: *Leptomithrax*, *Acanthophrys*.

#### Subfamily OPHTHALMIINAE

ZOEA: Carapace lateral spines present; dorsal spine very short; rostral spine very short; more than one spine<sup>1</sup> on each telson fork; abdominal dorso-lateral processes absent; ? 3 prominent dorso-lateral setae on 1st abdominal segment; postero-lateral processes on 3rd–5th abdominal segments absent; basal segment of 2nd maxilliped ? without setae; antennal exopod with terminal<sup>2</sup> setae.

MEGALOPA: Rostrum present, well developed, straight; submedian spines or processes absent; cardiac spine absent; basal segment of 2nd pereopod ? without spines.

GENERA: *Stilbognathus*



## Subfamily MITHRACINAE

ZOEA (group I): Carapace lateral spines absent; dorsal spine of moderate length; rostral spine short; only one spine<sup>1</sup> on each telson fork; dorso-lateral process on 2nd abdominal segment; postero-lateral processes on 3rd–5th abdominal segments sometimes short; basal segment of 2nd maxilliped ? without setae; antennal exopod with sub-terminal<sup>3</sup> setae (? except in *Mithrax*).

MEGALOPA (group I): Rostrum present, deflected slightly ventrally; submedian processes present; cardiac spine reduced; basal segment of 2nd pereopod ? without spines; uropod present.

GENERA: *Microphrys*, *Mithrax*, *Tiarinia*.

ZOEA (group II): Carapace lateral spines present; dorsal spine absent; rostral spine of moderate length; more than one spine<sup>1</sup> on each telson fork; dorso-lateral processes on 2nd–3rd abdominal segments; postero-lateral abdominal processes on 3rd–5th segments short; basal segment of 2nd maxilliped ? without setae; antennal exopod with sub-terminal<sup>3</sup> setae.

MEGALOPA (group II): Rostrum present, deflected slightly ventrally; submedian processes absent; cardiac spine absent or reduced; basal segment of 2nd pereopod with a spine; uropods present.

GENUS: *Micippa*.

The subfamilial larval features listed above reveal considerable degrees of apparent phylogenetic homology within three of the six subfamilies (i.e. Oregoniinae, Acanthonychinae and Pisinae) of the Majidae. This homology is less clear within the remaining subfamilies except, perhaps, the Inachinae in which two groups can be recognized that correspond to the divisions of this subfamily proposed by Balss (1929), the Camposcioidea (group I) and the Macrocheiroidea (group II). These divisions were partly (see Garth, 1958) and totally (see Griffin, 1966) rejected by subsequent workers because of the difficulties in interpreting homologies of orbital spines in genera and species assigned to one or the other group. Similar relationships of larvae attributed to the subfamilies Majinae and Mithracinae are not apparent at present and no doubt reflect our limited larval knowledge of these two subfamilies. Nevertheless, this present evaluation seems to suggest multiple phylogenetic lineage for both subfamilies and perhaps similar to that shown for the Inachinae.

Larval affinities of *Rochinia carpenteri*

In having prominent lateral spines on the carapace and ten setae on the basis of the first maxilliped, the first zoea of *R. carpenteri* shows affinities to the Oregoniinae rather than to the other subfamilies of Majidae in which the lateral spines are sometimes absent and in which the first maxilliped basis often has less than ten setae. The single spine on each fork of the telson and the sub-terminal setae on the antennal exopod place the zoea of *R. carpenteri* near to the Acanthonychinae, some group I Inachinae and to the Pisinae. Its affinities to the Pisinae are further strengthened by the setal armature of the first maxilliped basis (10) and the moderately developed spinous processes of the postero-lateral margins of the third to fifth abdominal segments. The megalopa of *R. carpenteri* is more difficult to assign but the well developed rostral spine, the absence of submedian spines or processes and the prominent cardiac spine all suggest tenuous affinities to some inachinid (i.e. *Macrocheira*) and pisinid (i.e. *Libinia*) megalops.

## Larval bibliography of the family Majidae

## OREGONIINAE

*Chionoecetes bairdi* Rathbun

Haynes, 1973 : 769, figs 1–2 (prezoea, 1st zoea); Jewett & Haight, 1977 : 459 (megal.)

*Chionoecetes japonicus* Rathbun

Motoh, 1970 : 7 (descript prezoea & 1st zoea); Motoh, 1976 : 533, figs 1–4 (1st, 2nd zoeae, megal.)



*Chionoecetes opilio* (Fabricius)

non Stephensen, 1935 : 40, fig. 16 (= ? *Geryon* sp.); Aikawa, 1935 : 222, Pl. I, fig. 5 (prezoea); Aikawa, 1937 : III, fig. 17 (prezoea); Kurata, 1963 : 25, fig. 1 (1st, 2nd zoeae, megal.); Kon, 1967 : 727, fig. 1, Pl. I (prezoea, 1st zoea); Ito, 1968 : 91 (descript. prezoea); Kuwatani *et al.*, 1971 : 32, Pls 1-3 (prezoea, 1st zoea as *C. opilio elongatus*); Kuwatani *et al.*, 1973 : 93, fig. 1 (prezoea); Haynes, 1973 : 774, fig. 2l, m (1st zoea); Motoh, 1973 : 1223, figs 1-4 (1st, 2nd zoea, megal.)

*Hyas araneus* (Linnaeus)

Björck, 1913 : 22, figs 1, 2 (megal. as *H. coarctatus*); Williamson, 1915 : 526, figs 424-5 (megal. after Björck as *Inachus coarctatus*); Lebour, 1928 : 544, Pl. XIV, fig. 10 (1st crab as *H. coarctatus*); Lebour, 1931 : 93, Pl. II, fig. 1 (1st zoea); Christiansen, 1973 : 67, figs 1A-19A (1st, 2nd zoeae, megal. 1st, 2nd crab)

*Hyas coarctatus* Leach

Williamson, 1911 : 13, Pl. I, figs 1, 2, Pl. V, figs 70-81, 83 (1st, 2nd zoea, megal. 1st crab as *H. araneus*); Stephensen, 1912 : 127, fig. 33 (1st zoea as Brachyurid-larvae); Williamson, 1915 : 521, figs 409-417 (1st, 2nd zoeae as *Inachus araneus*); Williamson, 1915 : 526, figs 420-423, 426-429 (1st, 2nd zoeae); Stephensen, 1917 : 241, fig. 1 (2nd zoea); Lebour, 1928 : 544, fig. 4 (14-15), fig. 5 (29-30) Pl. II, fig. 9, Pl. XIV, figs 8-9 (1st, 2nd zoeae, megal.); Kurata, 1963 : 28, fig. 2 (1st, 2nd zoea, megal. as *H. coarctatus alutaceus*); Christiansen, 1973 : 67, figs 1B-19B (1st, 2nd zoea, megal. 1st, 2nd crab)

*Hyas lyratus* Dana

Hart, 1960 : 542, figs 29-38 (1st, 2nd zoeae, megal.)

*Oregonia gracilis* Dana

Hart, 1960 : 540, figs 1-28 (1st, 2nd zoeae, megal.)

## ACANTHONYCHINAE

*Acanthonyx lunulatus* (Risso)

Cano, 1893 : 539, Tav. 35, figs 60-63 (2nd zoea as *Acanthonyx* sp.); Boraschi, 1921 : 8, Tav. I, fig. 4 (1st zoea); Bourdillon-Casanova, 1960 : 214, fig. 73 (1st, 2nd zoeae); Heegaard, 1963 : 482, figs 112-118, Pl. XVII, fig. 21 (1st zoea)

*Acanthonyx petiverii* H. Milne Edwards

Lebour, 1944 : 120, fig. 10 (1st zoea)

*Epialtus dilatatus* A. Milne Edwards

Yang, 1968 : 181, figs 1-8 (1st, 2nd zoeae, megal. 1st crab)

*Huenia proteus* de Haan

Aikawa, 1935 : 220, Pl. I, fig. 4 (1st zoea); Aikawa, 1937 : 108, fig. 15 (1st zoea); Kurata, 1969 : 98, fig. 11 (1st zoea)

*Menaethius monoceros* (Latreille)

Gohar & Al-Kholy, 1957 : 194, Pl. VIII (1st, 2nd zoeae, megal.)

*Pugettia gracilis* (Dana)

Forss & Coffin, 1960 : 4, Pls III, IV (1st zoea, megal.)

*Pugettia incisa* (de Haan)

Kurata, 1969 : 96, figs 9, 10 (1st zoea, megal.)

*Pugettia quadridens* (de Haan)

Aikawa, 1927 : 270, Pl. I (1st zoea); Aikawa, 1929 : 38, Pl. III, fig. 19, Pl. IV, figs 25, 33 (1st zoea); Kurata, 1969 : 94, figs 7, 8 (1st zoea, megal.); Iwata, 1970 : 189, fig. 1, Pl. I-II (prezoea, 1st zoea)

*Taliepus dentatus* (A. Milne Edwards)

Fagetti & Campodonico, 1971 : 1, figs 1-3 (1st, 2nd zoea, megal.)

## INACHINAE

*Achaeus cranchii* Leach

Bocquet, 1954 : 50, figs 1-4 (1st, 2nd zoeae, megal.)

*Achaeus tuberculatus* Miers

Kurata, 1969 : 87, figs 2, 3 (1st zoea, megal. 1st crab)

*Achaeus* spp.

Aikawa, 1935 : 218, 219, Pl. I, figs 1, 2 (1st zoeae); Aikawa, 1937 : 107, 108, figs 13, 14 (1st zoeae); Bourdillon-Casanova, 1960 : 220, figs 76-77 (megal. 1st crab)

*Anasimus latus* Rathbun

Sandifer & van Engel, 1972 : 141, figs 1-4 (1st, 2nd zoeae, megal.)

*Camposcia retusa* Latreille

Gohar & Al-Kholy, 1957 : 189, figs 1-3 (1st, 2nd zoeae, megal.)

*Eurypodius latreillei* Guérin

Italo Campodonico & Leonardo Guzman, 1972 : 233, figs 1-4 (1st, 2nd zoeae, megal.)

*Inachus dorsettensis* (Pennant)

Claus, 1876: Taf. X, fig. 8 (1st zoea as *I. scorpio*); non Cano, 1893: Tav. 35, fig. 71 (1st zoea as *I. scorpio* = *I. thoracicus*); non Williamson, 1915 : 530, fig. 430 (1st zoea after Cano = *I. thoracicus*); Lebour, 1927 : 802, Pls I-IV (prezoea, 1st, 2nd zoeae, megal. 1st crab); Lebour, 1928 : 546, Pl. III, fig. 5, Pl. XV, figs 4-5 (prezoea, 1st, 2nd zoeae, megal. 1st-3rd crab); Heegaard, 1963 : 471, figs 70-76, Pl. XVII, fig. 15 (1st zoea); Ingle, 1977 : 331, figs 1-10 (1st, 2nd zoeae, megal. 1st-3rd crab)

*Inachus leptochirus* Leach

Lebour, 1928 : 548, Pl. III, fig. 7, Pl. XIV, figs 11, 13, Pl. XV, figs 1, 2 (1st, 2nd zoeae, megal. 1st crab)

*Inachus phalangium* (Fabricius)

Gourret, 1884 : 17, Pl. I, figs 5-6 (1st zoea as *I. dorynchus*); Williamson, 1915 : 531, figs 431-432 (1st zoea as *I. dorynchus* after Gourret); Lebour, 1928 : 547, Pl. III, fig. 6, Pl. XIV, fig. 12, Pl. XV, fig. 3 (1st, 2nd zoeae, megal. as *I. dorynchus*)

*Inachus thoracicus* Roux

Heegaard, 1963 : 474, figs 77-83, Pl. XVII, fig. 16 (1st zoea)

*Inachus* spp.

Bourdillon-Casanova, 1960 : 215, figs 74-75 (megals, 1st crab)

*Macrocheira kaempferi* de Haan

Aikawa, 1941 : 119, fig. 2 (1st zoea); Tanase, 1967 : 303, figs 1-3 (1st, 2nd zoeae, megal.); Kurata, 1969 : 89, figs 4-5 (1st zoea, megal.)

*Macropodia deflexa* Forest

Lebour, 1928 : 550, Pl. III, fig. 9, Pl. XV, fig. 6, Pl. XVI, figs 1, 2, 7 (prezoea, 1st, 2nd zoeae, megal. 1st crab as *M. egyptia*)

*Macropodia rostrata* (Linnaeus)

Thompson, 1836 : 371, fig. 1e (1st zoea as *M. phalangium*); Cano, 1893: Tav. 35, figs 70-74, 77-83 (1st zoea, megal. crab stage as *Stenorhynchus phalangium*); Lo Bianco, 1904 : 33, Taf. XII, fig. 43 (1st crab as *S. phalangium*); Lebour, 1928 : 550, Pl. III, fig. 10, Pl. XV, fig. 7, Pl. XVI, figs 3, 5, 8 (prezoea, 1st, 2nd zoeae, megal. 1st crab)

*Macropodia tenuirostris* (Leach)

Lebour, 1927 : 806, Pl. I, figs 2, 8, Pl. II, fig. 2, Pl. III, figs 2, 4, 5 (prezoea, 1st, 2nd zoeae, megal. 1st crab as *M. longirostris*)

*Naxia hystrix* Miers

Aikawa, 1935 : 222, Pl. I, fig. 6 (1st zoea); Aikawa, 1937 : 109, fig. 16 (1st zoea)

*Paratymolus pubescens* Miers

Aikawa, 1937 : 106, fig. 12 (1st zoea)

*Pleistacantha sancti-johannis* Miers

Aikawa, 1935 : 220, Pl. I, fig. 3 (1st zoea); Aikawa, 1937 : 105, fig. 11 (1st zoea); Kurata, 1969 : 92, fig. 6 (1st zoea)

*Stenorhynchus seticornis* (Herbst)

Yang, 1976 : 158, figs 1-9 (1st, 2nd zoeae, megal. 1st crab)

*Stenorhynchus* sp.

Yang, 1976 : 168, figs 11-13 (1st zoea)

## PISINAE

*Doclea gracilipes* Stimpson

Chhapgar, 1959 : 48, fig. 11 (megal.)

*Eurynome aspera* (Pennant)

\*Kinahan, 1858 : 233 (prezoea); \*Kinahan, 1860 : 73, Pl. 9, figs 4-6 (? 1st zoea); Cano, 1893 : Taf. 35, figs 57-59 (1st zoea as *Eurynome* sp.); \*Gurney, 1924 : 433, figs 1-2 (prezoea, 1st zoea); \*Lebour, 1928 : 543, fig. 5 (31), Pl. II, fig. 8, Pl. XIV, figs 2-5 (1st, 2nd zoeae, megal. 1st crab); Bourdillon-Casanova, 1960 : 204, fig. 67a (megal.)

*Herbstia condyliata* (Herbst)

Cano, 1893 : Tav. 35, figs 52-56 (2nd zoea, megal.); Bourdillon-Casanova, 1960 : 205, fig. 68 (1st zoea)

*Hyastenus diacanthus* (de Haan) Kurata, 1969 : 101, figs 13-14 (1st zoea, megal.)

*Libidoclaea grandaria* H. Milne Edwards & Lucas

Fagetti, 1969 : 131, figs 1-4 (1st, 2nd zoeae, megal.)

*Libinia dubia* H. Milne Edwards

Sandifer & van Engel, 1971 : 18, figs 1-4 (1st, 2nd zoeae, megal.)

*Libinia emarginata* Leach

Johns & Lang, 1977 : 831, figs 1-5 (1st, 2nd zoeae, megal.)

*Libinia setosa* Lockington

Rathbun, 1923 : Pl. XXXVI, fig. 1 (megal.)

*Libinia spinosa* H. Milne Edwards

Boschi & Scelzo, 1968 : 170, figs 1-42 (1st, 2nd zoeae, megal.)

*Lissa chiragra* (Herbst)

Cano, 1893 : Tav. 35, figs 45-51 (1st, 2nd zoeae, megal. 1st crab as *Lissa* sp.); Boraschi, 1921 : 8, Tav. 1, fig. 15 (1st zoea); Bourdillon-Casanova, 1960 : 212, fig. 72 (1st zoea); Heegaard, 1963 : 480, figs 105-111, Pl. XVII, fig. 20 (1st zoea)

*Naxioides histrix* (Miers)

Kurata, 1969 : 100, fig. 12 (1st zoea)

*Naxioides serpulifera* (Guérin)

Rathbun, 1914 : 661, Pl. II, figs 9-10 (1st, 2nd crab, direct develop.)

*Pisa armata* (Latreille)

Lebour, 1931 : 94, Pl. II, fig. 2, Pl. I, figs 2-5 (1st, 2nd zoeae as *P. biaculeata*); Bourdillon-Casanova, 1960 : 207, fig. 69 (megal. as *P. gibbsi*); Heegaard, 1963 : 476, figs 84-90, Pl. XVII, fig. 17 (1st zoea)

*Pisa corallina* (Risso)

Gourret, 1884 : 15, Pl. II, figs 3-5 (1st zoea)

\* Identity uncertain because of confusion with *E. spinosa* (see Hartnoll, 1961).

*Pisa nodipes* Leach

Heegaard, 1963 : 479, figs 98–104, Pl. XVII, fig. 19 (1st zoea)

*Pisa tetraodon* (Pennant)

Heegaard, 1963 : 477, figs 84–90, Pl. XVII, fig. 18

*Pisa* spp.

Cano, 1893 : Tav. 35, figs 41–44 (1st, 2nd zoeae, megal.? crab stage); Bourdillon-Casanova, 1960 : 210, fig. 70 (1st zoeae, megal.)

*Pisoides edwardsi* (Bell)

Fagetti, 1969a : 160, figs 1–3 (1st, 2nd zoeae, megal.)

*Pisoides ortmanni* (Balss)

Kurata, 1969 : 103, figs 15, 16 (1st zoea, megal.)

## MAJINAE

*Acanthophrys longispinosus* (de Haan)

Kurata, 1969 : 111, figs 22, 23 (1st zoea, megal.)

*Leptomithrax bifidus* Ortmann

Kurata, 1969 : 106, figs 18, 19 (1st zoea, megal.)

*Leptomithrax edwardsi* (de Haan)

Kurata, 1969 : 105, fig. 17 (1st zoea)

*Maja squinado* (Herbst)

Schlegel, 1911 : 480 (1st, 2nd zoeae, megal. descript. only); Lebour, 1927 : 809, Pl. I, figs 3, 9, Pl. II, figs 3, 9, Pl. II, figs 3, 9, Pl. IV, figs 9–15 (prezoea, 1st, 2nd zoeae, megal. not crab stages = portunids); Lebour, 1928 : 542, figs 2 (1–2), Pl. II, fig. 7, Pl. XIV, figs 6–7 (1st, 2nd zoeae, megal. not 1st–3rd crab = portunids); Bourdillon-Casanova, 1960 : 203, fig. 66 (megal.)

*Maja verrucosa* H. Milne Edwards

Cano, 1893 : Tav. 34, figs 26–28 (not fig. 29 = *Sirpus*, see Gordon 1953), fig. 30, Tav. 35, fig. 86 (1st, 2nd zoeae, megal. crab stage); Bourdillon-Casanova, 1960 : 202 (cf 1st, 2nd zoeae with *M. squinado*); Heegaard, 1963 : 484, figs 119–126, Pl. XVII, fig. 22 (1st zoea)

*Schizophrys aspera* (H. Milne Edwards)

Kurata, 1969 : 108, figs 20, 21 (1st zoea, megal.)

## Majinae

Rice & Williamson, 1977 : 41, fig. 17 (2nd zoea)

## OPHTHALMIINAE

*Stilbognathus erythraceus* von Martens

Al-Kholy, 1959 : 240, figs 1–21 (2nd zoea, megal.)

## MITHRACINAE

*Micippa thalia* (Herbst)

Kurata, 1969 : 113, figs 24, 25 (1st zoea, megal.)

*Microphrys bicornutus* (Latreille)

Lebour, 1944 : 122, fig. 12 (1st, 2nd zoeae); Hartnoll, 1964 : 241, figs 1–3 (prezoea, 1st, 2nd zoeae)

*Mithrax forceps* A. Milne Edwards

Lebour, 1944 : 121, fig. 11 (1st zoea)

*Mithrax spinosissimus* (Lamarck)

Provenzano & Brownell, 1977 : 735, figs 1–7 (1st, 2nd zoeae, megal. 1st crab)

*Tiarinia cornigera* Latreille

Aikawa, 1937 : 112, fig. 18 (1st zoea); Kurata, 1969 : 115, fig. 26 (1st zoea)



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